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# THE UREDINALES FOUND UPON THE ONAGRACEAE

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The members of the family Onagraceae, while of cosmopolitan distribution, are particularly American. Western North America is especially rich in species belonging to this family. Similarly, while a few rusts upon members of the Onagraceae are scattered over many parts of the world, the majority of them are known only from America. The Sydows, in the three published volumes of their Monograph of the Uredinales, list 27 species of rusts upon the Onagraceae. Of these, 15 species are given as existing only in North America, 3 species only in South America, and 2 species both in America and in other countries. Of the species for which the Americas are not included as localities, 3 have been found to be present. Thus, of the 27 species listed by the Sydows, 23 occur in the Western Hemisphere, and 21 of these have been found in North America. In addition to the species published in the Sydows' monograph, there are *Aecidium Anograe* and *Puccinia Fuchsiae*, both known only from North America. *Puccinia Veratri*, a widely distributed species, has rather recently been found to have its aecial stage upon certain of the Onagraceae; the telial stage only is listed in Sydow, and not included above. *Puccinia Nesaeae* (Ger.) Ell. & Ev., listed in Sydow as occurring upon Nesaea, is misplaced, the host in reality being Ludwigia, a genus of the Onagraceae.

The family Onagraceae has proved perplexing to the phanerogamic taxonomists; a glance at the lack of uniformity in ideas of nomenclature and arrangement of species as represented in various floras attests to the uncertainty of specific characters in this group of plants. These very uncertainties and variabilities have given this family important consideration from an evolutionary standpoint. An extensive literature has grown around the genus Oenothera alone.

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So, too, the rusts occurring upon these hosts have been found to be variable, uncertain, and confusing. Arthur[1] has dealt with similar conditions in the case of the rose rusts, in which the variability of the host appears to be reflected in a similar degree by the variation in the rust. In his discussion of this condition Arthur states (p. 28) that "each species of Phragmidium has attained a degree of orthogenetic development and a diversity of characters corresponding to the hosts on which it occurs, always, however, with a certain lag due to the inhibiting nature of parasitism." It would seem that parallel conditions as regards variability, both with the hosts and their rusts, obtain in both the Rosaceae and Onagraceae.

Considerable work has been done upon the rusts of the Onagraceae; the results, however, are rather scattered and somewhat conflicting, and the species described have seemed often to be of doubtful validity. The Sydows, as previously suggested, have done much toward systematizing the knowledge of these rusts; Holway has published valuable descriptions and notes on the species of Puccinia occurring upon this group. Descriptions of some of these rusts have already appeared in the North American Flora. Many other writers have added their ideas; yet it was apparent that further work upon a considerable number of collections of some of these species of rust should result in an attainment of greater order. The facilities of the Arthur herbarium have afforded to the writer an unequaled opportunity to study a large number of collections; preparation of manuscript upon the rusts for the North American Flora rendered it imperative that additional critical studies be made of Onagraceous rusts.

The ideas regarding relationship, correlation, and classification, advocated in this paper, should be considered but the elaboration of the opinions held by Dr. J. C. Arthur, and by the workers in his laboratory. It has been possible to bring together the data presented, through the courtesy of Dr. Arthur in placing the facilities of the laboratory at the writer's disposal. Furthermore, thanks are due to Messrs. F. D. Kern, C. R. Orton, C. A. Ludwig, and especially to Prof. H. S. Jackson, for much assistance.

The term "correlation," as used in this paper and by other writers from this laboratory, is intended to express an idea of relationship of rusts based on similarities of morphological characters. This simi-

[1] Arthur, J. C., North American Rose Rusts. Torreya 9: 21–28. 1909.

larity may be expressed in different ways. One of the earliest noted resemblances between species was that between certain Uromyces and Puccinia forms with the same life cycle, the only difference being in the possession, by the one species, of one-celled teliospores, by the other of two-celled teliospores. Fries[2] noted the fact that such an analogy sometimes existed. Orton[3] has reviewed the literature pertaining to this type of correlation, and shown some specific instances. This kind of correlation is shown in the Onagraceae rusts by the resemblance of *Uromyces plumbarius* to *Puccinia Epilobii-tetragoni*.

A second type of correlation is that illustrated by a similarity in the characters of a short-cycled species and a long-cycled heteroecious species bearing aecia upon the telial host of the short-cycled rust. Dietel,[4] and about the same time, Fischer,[5] pointed out this type of resemblance. Travelbee,[6] from this laboratory, has briefly summarized the literature regarding this type of correlation, and listed some proven examples. This indicated relation has been successfully used to predict alternate hosts: indeed, in the Onagraceae rusts, through the similarity of the telial stage of *Puccinia Epilobii* to that of *Puccinia Veratri*, the alternate host of the latter was forecasted, as is noted later in this article.

A third type of correlation is that between two species of rust, with life cycles of different lengths, occurring upon the same or similar hosts. Fischer[7] has indicated such a relation between two species of rust upon Epilobium; other possibilities are suggested in this paper.

It is obvious that a similarity of morphological characters does not of necessity reflect a phylogenetic relationship. Certainly, however, when such similarities are found between rusts upon related hosts, it is a noteworthy suggestion of a definite relationship between the rusts, and it seems to the writer that relationships may be inferred in certain cases even when there is some slight variation between the parallel characters of two such species of rust.

Races are designated in this paper as occurring within the long-

[2] Fries, E. M., Summ. Veg. Scand. 1: 514. 1846.

[3] Orton, C. R., Correlation between certain species of Puccinia and Uromyces. Mycol. 4: 194–204. 1912.

[4] Dietel, P., Uredinales, in Engler and Prantl, Pflanzenfam. $1^{1++}$: 69. 1897.

[5] Fischer, Ed., Beitr. Krypt. Schweiz $1^{1}$: 109. 1898.

[6] Travelbee, H. C., Correlation of certain long-cycled and short-cycled rusts. Proc. Ind. Acad. Sci. 1914: 231–234. 1915.

[7] Fischer, Ed., Beitr. Krypt. Schweiz $2^{2}$: 154–155. 1904.

cycled autoecious species discussed. The idea embodied is somewhat different from that of physiological or biological races. The latter designation of races is used, in the Uredinales, in cases where cultures have shown that there are certain restrictions upon the transference of a rust from host to host. The idea made use of here is that of morphological races—races separated upon the same ideas of differentiation upon which species are ordinarily based, but the differences being not of sufficient value nor constancy to make possible a separation into species. In the absence of cultural data, these races are suggested for convenience. The idea is somewhat that of varieties under a species. The word variety is not used, however, as that would result in a cumbersome, and perhaps inaccurate, nomenclature; a tentative division into morphological races seems to afford an opportunity to systematize the arrangement of specimens representing rather variable species.

A perfectly consistent treatment of the evening primrose rusts, embracing all the species, is now impossible. This study is therefore made primarily in an attempt to draw attention to some of the questions demanding answer, and in the hope that collections, cultures, and studies may eventually be made to clarify and arrange our knowledge of this interesting group of rusts.

The main points brought out in this paper are: the grouping together of the long-cycled autoecious forms of Puccinia upon the Onagraceae into one species, and the considerations involved; some notes upon the heteroecious forms which include the Onagraceae in their life cycle; some correlations indicated between different species and races; keys to aid in the diagnosis of the various rusts in question. Several incidental points are discussed. Species not known in North America are dealt with only briefly. Descriptions of several of the species under discussion are not added here, since that would appear to be an unnecessary duplication. References to descriptions easily available are given in such cases.

The keys herewith presented offer difficulties at some points, due partly, as pointed out above, to the fact that correlated species possess spore-forms morphologically indistinguishable. The different considerations, however, usually can be utilized to place a specimen. The abbreviations N.A. (North America), S.A. (South America), Eur. (Europe), etc., and the symbols O (pycnia), I (aecia), II (uredinia), and III (telia), used in places, are for brevity.

KEY, BASED UPON LIFE HISTORY

| | |
|---|---|
| Pycnia and aecia only occurring upon Onagraceae. | |
| Aecia diffused. | *Puccinia Veratri.* |
| Aecia in groups. | |
| Aeciospore wall thick, 2–3 μ. | *Aecidium Anograe.* |
| Aeciospore wall thin, 1 μ. | |
| Spores larger, 14–21 μ long. | *Puccinia Peckii.* |
| Spores smaller, 13–15 μ long (Eur.) | *Aecidium Circaeae.* |
| Pycnia, aecia, and telia occurring upon Onagraceae. | |
| Teliospores up to 60 μ in length. | *Puccinia Jussiaeae* (*Puccinia Ludwigiae*). |
| Teliospores up to 45 μ in length (Eur.) | *Puccinia Epilobii-Fleischeri.* |
| Pycnia, aecia, uredinia, and telia occurring upon Onagraceae. | |
| Teliospores one-celled. | *Uromyces plumbarius.* |
| Teliospores two-celled. | *Puccinia Epilobii-tetragoni.* |
| Characters of the latter (S. A.) | *Puccinia luxurians.* |
| Life-history uncertain; possibly same as *P. Epilobii-tetragoni* (Afr.) | *Puccinia Krookii.* |
| Uredinia and telia only occurring upon Onagraceae. | |
| Telia within or below epidermis. | *Pucciniastrum pustulatum.* |
| Characters similar to the latter (Eur.). | *Pucciniastrum Circaeae.* |
| Pycnia (when formed) and telia occurring upon Onagraceae. | |
| Teliospore apex scarcely thickened, 1.5–4 μ. | |
| Teliospore wall smooth, 3 μ thick. | *Puccinia sphaeroidea?** |
| Teliospore wall verrucose, 1.5–2 μ thick. | |
| Teliospores smaller, 13–18 by 27–37 μ. | *Puccinia scandica.* |
| Teliospores larger, 17–25 by 30–44 μ. | *Puccinia Epilobii.* |
| Teliospore apex considerably thickened, 5–12 μ. | |
| Teliospores somewhat smaller, up to 40 μ. | *Puccinia Circaeae.* |
| Teliospores medium, up to 50 μ. | *Puccinia Fuchsiae.* |
| Teliospores somewhat larger, up to 60 μ. | *Puccinia gigantea.* |
| Uredinia only known upon Onagraceae (S. A.). | *Uredo oenothericola.* |

KEY, BASED UPON SPORE FORMS INDEPENDENTLY

| | |
|---|---|
| Aecia in groups, *i. e.*, infection local. | |
| Aecisopore wall thick, 2–3 μ. | *Aecidium Anograe.* |
| Aeciospore wall thin, ¹ μ. | |
| Aecia small, 0.2–0.3 mm. across. | |
| Aeciospores 15–21 μ long. | *Puccinia Jussiaeae* (*Puccinia Ludwigiae*). |
| Aeciospores 13–15 μ long. | *Aecidium Circaeae.* |
| Aecia larger, 0.3–0.6 mm. across. | *Puccinia Peckii.* |

* Doubtfully upon Onagraceae.

| | |
|---|---|
| Aecia diffused, *i. e.*, infection general. | |
| Morphological characters similar; correlated species; aeciospores usually only to 20–21 $\mu$ in length. | *Uromyces plumbarius*, *Puccinia Epilobii-tetragoni*, *Puccinia Epilobii-Fleischeri* |
| Similar to above, except aeciospores often up to 23–24 $\mu$. | *Puccinia Veratri.* |
| Uredinia without peridium; urediniospore-wall colored. | |
| Uredinia often gregarious on spots. | *Uredo oenothericola.* |
| Uredinia scattered; spots none; correlated. | *Uromyces plumbarius*, *Puccinia Epilobii-tetragoni*, (*Puccinia luxurians*, *P. Krookii*). |
| Uredinia with peridium; urediniospore-wall colorless. | |
| Characters similar. | *Pucciniastrum pustulatum*, *Pucciniastrum Circaeae.* |
| Telia within or below epidermis. | |
| Characters similar. | *Pucciniastrum pustulatum*, *Pucciniastrum Circaeae.* |
| Telia erumpent. | |
| Teliospores one-celled. | *Uromyces plumbarius.* |
| Teliospores two-celled. | |
| Teliospore apex considerably thickened, 4–12 $\mu$. | |
| Telia scattered, not upon spots. | |
| Characters similar; correlated. | *Puccinia Epilobii-tetragoni*, *Puccinia Epilobii-Fleischeri.* |
| Characters apparently those of *Puccinia Epilobii-tetragoni.* | (*Puccinia luxurians* *Puccinia Krookii*). |
| Telia gregarious, upon spots. | |
| Teliospores smaller, to 40 $\mu$ long. | *Puccinia Circaeae.* |
| Teliospores to 50 $\mu$ long. | *Puccinia Fuchsiae.* |
| Teliospores larger, to 60 $\mu$ long. | |
| Wall cinnamon-brown. | *Puccinia Jussiaeae* (*Puccinia Ludwigiae*). |
| Wall paler, especially below. | *Puccinia gigantea.* |
| Teliospore apex little thickened, 1.5–4 $\mu$. | |
| Teliospore wall smooth, 3 $\mu$ thick. | ?*Puccinia sphaeroidea.* |
| Teliospore wall verrucose, 1.5–2 $\mu$ thick. | |
| Teliospores comparatively smaller, 13–18 by 27–37 $\mu$. | *Puccinia scandica.* |
| Teliospores comparatively larger, 17–25 by 30–44 $\mu$. | *Puccinia Epilobii.* |

KEY TO SPECIES AND RACES, BASED UPON HOST AND INCLUDING GEOGRAPHIC DISTRIBUTION

*Gayophytum;* N. A., S. A.; O, I, II, III, *Puccinia Gayophyti* race of *Puccinia Epilobii-tetragoni.*

*Chamaenerion*

Western N. A.; Eur.; O, I, II, III;
III spores to 40 μ, I spores usually to 20 μ.
*Puccinia Gayophyti* race of *Puccinia Epilobii-tetragoni.*

N. A.; Eur.; O & I
I often to 24 μ. *Puccinia Veratri.*

N. A.; Eur.; II & III only;
III spores often within epidermis. *Pucciniastrum pustulatum.*

Western N. A.; Eur.; III only;
III spores to 60 μ. *Puccinia gigantea.*

*Epilobium*

Teliospore apex thickened.
As first three under *Chamaenerion.* { *Puccinia Gayophyti* race of *Puccinia Epilobii-tetragoni*, *Puccinia Veratri*, *Pucciniastrum pustulatum.*
Eur.; O, I, III. *Puccinia Epilobii-Fleischeri.*
Afr.; uncertain. *Puccinia Krookii.*

Teliospore apex little thickened
N. A.; Eur.; III only,
III spores 13–18 by 27–37 μ. *Puccinia scandica.*
III spores 17–25 by 30–44 μ. *Puccinia Epilobii.*

*Boisduvalia glabella* only; Western N. A.; (O, I), II, III.....*Puccinia glabella* race of *Puccinia Epilobii-tetragoni.*

*Taraxia;* Western N. A.; O, I, II, III
*Puccinia heterantha* race of *Puccinia Epilobii-tetragoni.*

*Boisduvalia* (*P. Boiduvaliae*)
*Chylisma* (*P. Oenotherae*)
*Eulobus* (*P. Eulobi*)
*Clarkia*, *Godetia*, *Phaeostoma* (*P. Clarkiae*)
*Sphaerostigma* (*P. Sphaerostigmatis*)
*Zauchneria* (*P. Zauchneriae*)
} O, I, II, III; Western N. A.; *Puccinia Oenotherae* race of *Puccinia Epilobii-tetragoni.*

*Gaura*

N. A.; O, I, II, III; aecia diffused *Uromyces gauri-nus* race of *Uromyces plumbarius.*

N. A.; O, I; aecia grouped. *Puccinia Peckii.*

*Kneiffia;* N. A., O, I, II, III.
*Uromyces Oenotherae* race of *Uromyces plumbarius.*

*Oenothera*

N. A.; O, I, grouped. *Puccinia Peckii.*

N. A.; O, I, II, III; aecia diffused.
III spores one-celled.
*Uromyces Oenotherae* race of *Uromyces plumbarius.*
III spores two-celled.
?*Puccinia Oenotherae* race of *Puccinia Epilobii-tetragoni.*

| | |
|---|---|
| S. A.; O, I, II, III (?). | *Puccinia luxurians.* |
| S. A.; II only known. | *Uredo oenothericola.* |
| *Luxavia;* N. A.; O, I, II, III. | |
| | *Uromyces plumbarius* race of *Uromyces plumbarius.* |
| *Pachylopus* | |
| N. A.; O, I, II, III; aecia diffused | |
| | *Uromyces plumbarius* race of *Uromyces plumbarius.* |
| N. A.; O, I; aecia grouped. | *Puccinia Peckii.* |
| *Onagra* | |
| N. A.; O, I, II, III; aecia diffused | |
| | *Uromyces plumbarius* race of *Uromyces plumbarius.* |
| N. A.; O. I; aecia grouped. | *Puccinia Peckii.* |
| *Megapterum*, N. A.; O, I, II, III | |
| | *Uromyces Fremontii* race of *Uromyces plumbarius.* |
| *Meriolix*, N. A.; O. I. | *Puccinia Peckii.* |
| *Circaea* | |
| N. A.; Eur.; III; III erumpent | *Puccinia Circaeae.* |
| Eur.; II, III; III not erumpent. | *Pucciniastrum Circaeae.* |
| Eur.; O, I. | *Aecidium Circaeae.* |
| *Anogra*, central U. S.; O, I. | *Aecidium Anograe.* |
| *Jussiaea* | |
| N. A.; S. A.; I, III; spores up to 54 $\mu$ long. | *Puccinia Jussiaeae* (*Puccinia Ludwigiae*). |
| Western N. A.; III only; spores up to 32 $\mu$ long..... | ?*Puccinia sphaeroidea.* |
| *Ludwigia*, N. A.; O, I, III. | *Puccinia Jussiaeae* (*Puccinia Ludwigiae*). |
| *Fuchsia*, Mexico; III only. | *Puccinia Fuchsiae.* |

1. AECIDIUM ANOGRAE Arthur, Bull. Torrey Club **28**: 664. 1901.

O. Pycnia amphigenous, grouped on the spots with the aecia, inconspicuous, subepidermal, honey-yellow becoming brownish, globose, 100–120 $\mu$ in diameter by 80–100 $\mu$ in height; ostiolar filaments 30–80 $\mu$ long.

I. Aecia amphigenous, chiefly hypophyllous, gregarious on roundish or irregular reddened spots, cylindrical, 0.2–0.3 mm. in diameter by 0.5–0.6 mm. in height; peridium white, margin erect, toothed; peridial cells rectangular, 18–24 by 22–35 $\mu$, slightly overlapping, the outer wall 6–10 $\mu$, striate, the inner wall 3–5 $\mu$, coarsely verrucose; aeciospores irregularly globoid or ellipsoid, 18–23 by 22–26 $\mu$; wall pale yellow, thick, 2–3 $\mu$, evenly verrucose.

ON ONAGRACEAE: *Anogra pallida* (Lindl.) Britt. (*Oenothera pallida* Lindl., *Anogra Vreelandii* Rydb.) Nebraska.

TYPE LOCALITY: Long Pine, Nebraska, on *Anogra pallida.*

DISTRIBUTION: Known only from the dry northwestern part of Nebraska.

EXSICCATI: Barth., Fungi Columb. *2601.*

Additional collections and data allow the above expansion of the original description. This Aecidium, at present known only from the

Niobrara river valley in Nebraska, is distinctive, possessing cylindrical aecia and large, thick walled aeciospores. The telial stage perhaps occurs upon some Monocotyledonous host; quite possibly upon a sedge or a grass. One possibility, judging by the codistribution of host and rust, appeared to be *Puccinia eminens* Kern on *Carex Backii* Boot. An unreported culture in this laboratory, was, however, unsuccessful, and no definite morphological characters of the two species serve to indicate a relation.

2. AECIDIUM CIRCAEAE Cesati & Mont., in Montague, Syll. Gen. Spec. Crypt.: 312. 1856.

SYNONYMY: *Caeoma epilobiatum* Link, in Willd., Sp. Pl. $6^2$: 59. 1825. (In part) *Aecidium Circaeae* Cesati in Rabenh. Herb. Mycol. No. 372. 1861.

LITERATURE: Winter, in Rabenh. Krypt. Fl. 1: 266. 1881. Saccardo, Syll. Fung. 7: 791. 1888. Schroeter, Pilze Schles. 1: 379. 1889. Klebahn, Krypt. Mark Brand $5^a$: 870. 1914.

This form, known only from Europe, on Circaea, has not yet been connected with a telial stage. Klebahn points to the fact that *Brachypodium silvaticum* Roem. & Schult. often grows in association, but he was unable to prove a connection with the rust *Puccinia Baryi* (Berk. & Br.) Winter. A comparison of these two forms fails to give a clue to a relationship between them.

The name *Caeoma epilobiatum* Link is used by Saccardo and by Klebahn as in part a synonym. This name is discussed further in this paper under *Puccinia Epilobii-tetragoni.*

3. PUCCINIASTRUM PUSTULATUM (Pers.) Dietel, in Engler & Prantl, Pflanzenfam. $1^{1++}$: 47. 1897.

DESCRIPTION: N. Amer. Fl. 7: 107. 1907.

LITERATURE: Saccardo, Syll. Fung. 7: 762. 1888. Schroeter, Pilze Schles. 1: 364. 1889. Klebahn, Krypt. Mark Brand. $5^a$: 831. 1914. Sydow, Monogr. Ured. 3: 444. 1915.

*Pucciniastrum Abieti-chamaenerii* Kleb. is united, in the North American Flora, with *Pucciniastrum pustulatum.* There are but slight differences in the morphological characters of the two species. Cultures, made in America since the publication of the description in the Flora, and substantiating European cultures, have been successful, however, only with the *Pucciniastrum Abieti-chamaenerii* form. It would seem, therefore, that the two forms might well now be considered as separate races.

Some confusion has existed concerning the synonymy of this species. Further study has shown that the synonymy, as given with the description in the North American Flora, should be revised as follows: *Uredo Epilobii* DC. in Lam. & DC. Fl. Franç. **6**: 73. 1815; and *Caeoma Epilobii* Link, in Willd. Sp. Pl. **6**$^2$: 29. 1825, are synonyms of *Puccinia Epilobii-tetragoni*, and are discussed in this paper under that species. In the place of *Caeoma Epilobii* in the Flora, should be listed *Caeoma Onagrarum* Link, in Willd. Sp. Pl. **6**$^2$: 29. 1825. (In part.) Following the latter name should be added *Erysibe pustulata Epilobium* Wallr., Fl. Crypt. Germ. **2**: 198. 1833. *Melampsora Chamaenerii* Rost., Medd. Bot. For. Kjöbenhavn. 1:·77. 1884 (nomen nudum; no description) might be added to the synonymy, and also *Pucciniastrum Chamaenerii* Rostr., Plantepatol. 304. 1902.

The aecia of *Pucciniastrum pustulatum* (or, more accurately, of *Pucciniastrum Abieti-chamaenerii*) were unknown in America at the date of publication in the North American Flora. Fraser (Mycol. **4**: 176–177. 1912) first cultured this rust in America. Aecia have been found upon Pinaceae in America, and are represented in the herbarium as follows: on *Abies balsamea* (L.) Mill., Nova Scotia, Fraser, 1911; Michigan, Kauffman, 1914; Vermont, Orton, 1913; Wisconsin, Cheney, 1906; on *Abies concolor* (Gord.) Parry, Colorado, Bethel, 1903, 1909, 1913; on *Abies grandis* Lindl., Oregon, Jackson, 1915; Idaho, Weir, 1915; on *Abies lasiocarpa* (Hook.) Nutt., British Columbia, Holway, 1907; Oregon, Jackson, 1914; Colorado, Bethel, 1915.

The aecia of this species as found in America, produce spores somewhat larger than those of European collections, being 13–18 by 17–23 $\mu$ here, and but 10–14 by 13–21 $\mu$ in Europe. No other difference is noted.

The range of the uredinia and telia of this species has also been extended, the following additions having been made since the publication in 1907: to *Chamaenerion angustifolium* (L.) Scop. add New Mexico, Oregon, West Virginia; Alberta, British Columbia, Nova Scotia. To *Epilobium adenocaulon* Haussk. add Idaho, North Dakota, Oregon, South Dakota, Utah, Virginia, Washington, West Virginia, Wisconsin, Wyoming; British Columbia. Add *Epilobium affine* Bong., Alaska. To *Epilobium anagallidifolium* Lam., add Utah. Add *Epilobium novomexicanum* Hausskn., New Mexico; *Epilobium californicum* Hausskn., California; and *Epilobium brevistylum* Barbey, Oregon.

4. PUCCINIASTRUM CIRCAEAE (Thüm.) Speg., Dec. Mycol. Ital. No. 65. 1879.

LITERATURE: Saccardo, Syll. Fung. 7: 763. 1888. Schroeter, Pilze Schles. 1: 364. 1889. Klebahn, Krypt. Mark Brand. 5ª: 833. 1914. Sydow, Monogr. Ured. 3: 445. 1915.

This European species upon Circaea presents no very tangible morphological differences from *Pucciniastrum pustulatum*. The hosts are different. Cultures, moreover, have so far failed to produce infection upon or from Abies, so that this species may well be considered to be distinct.

Klebahn (*l. c.*) gives some evidence for his suggestion that perhaps an overwintering of the rust occurs in the rhizomes of the host.

The synonym *Erysibe pustulata Circaeae* Wallr., Fl. Crypt. Germ. 2: 198. 1833, does not seem to appear in recent literature.

5. UROMYCES PLUMBARIUS Peck, Bot. Gaz. 4: 127. 1879.

DESCRIPTIONS: N. Amer. Fl. 7: 262. 1912. Sydow, Monogr. Ured. 1: 54–56. 1909.

This American species, treated here as in the North American Flora, represents a combination of four species described by different authors upon different species of host. This somewhat variable species falls into morphological races, corresponding in a general way with previously described species, as follows: (1) on *Gaura* (*Uromyces Gaurinus*). This race possesses teliospores of moderate size (16–23 by 24–33 $\mu$), with the apex thickened the least of those of any of the races, 4–7 $\mu$. A suggestion of verrucose markings can sometimes be seen upon the teliospores of this race. (2) On *Kneiffia* and *Oenothera* (*Uromyces Oenotherae*). This race is distinguished by dark-colored teliospores, with the apex the thickest of those of any of the races, 7–14 $\mu$. The apex is often pointed, and the pedicel length the greatest in this species. (3) On *Luxauvia*, *Pachylophus*, and *Onagra* (*Uromyces plumbarius*). This race has the smallest teliospores (14–20 by 21–28 $\mu$), with the apex but moderately thickened. The teliospores have been found to be very finely and inconspicuously verrucose, hardly noticeable unless the spores are viewed with the oil immersion. (4) On *Megapterium Fremontii* (*Uromyces Fremontii*). This race possesses teliospores with the thickest walls, sometimes to 3 $\mu$. The teliospores are comparatively narrow and long.

The correlation of this species and these races with the corre-

sponding autoecious long-cycled *Puccinia* is noted under *Puccinia Epilobii-tetragoni.*

The following additions may now be made to the range and hosts listed under the description in the Flora: add *Gaura induta* Woot. & Standley, New Mexico; add *Oenothera runcinata* (Engelm.) Small, New Jersey; to *Onagra biennis* add Delaware and Missouri; to *Pachylophus macroglottis* add Colorado; to *Pachylophus montanus* add Montana and Utah. To the exsiccati the following additions have appeared: Barth. Fungi Columb. *3893* and Barth. N. Am. Ured. *493*, *596*, *1396* and *1495*.

6. PUCCINIA EPILOBII-TETRAGONI (DC.) Winter, in Rabenh. Krypt. Fl. **1**: 214. 1881.

LITERATURE: Plowright, Monogr. Brit. Ured. 152–153. 1889. Sydow, Monogr. Ured. **1**: 423–435. 1903. Fischer, Beitr. Krypt. Schweiz $2^2$: 152–153. 1904. McAlpine, Rusts Austral. 170. 1906. Holway, N. Amer. Ured. **1**: 74–79. 1907. Bubak, Pilze Boehmens **1**: 67. 1908. Grove, Brit. Rust Fungi 198–200. 1913. Lind, Danish Fungi 319. 1913. Klebahn, Krypt. Mark Brand. $5^a$: 335–337. 1914. Saccardo, Syll. Fung., various volumes and pages, under the different names.

SYNONYMY:

*Uredo vagans* α *Epilobii-tetragoni* DC. Fl. Franç., **2**: 228. 1805.
*Aecidium Epilobii* DC. Fl. Franç., **2**: 238. 1805.
*Uredo Epilobii* DC. Fl. Franç., **6**: 73. 1815.
*Puccinia pulverulenta* Grev. Fl. Edinb. 432. 1824.
*Caeoma Epilobii* Link, in Willd. Sp. Pl. $6^2$: 29. 1825.
*Caeoma Epilobiatum* Link, in Willd. Sp. Pl. $6^2$: 59. 1825. p.p.
*Puccinia tenuistipes* Opiz, Seznam Rost. Kvét. Césté. 139. 1852.
*Trichobasis Epilobii* Berk. Outl. 333. 1860.
*Puccinia Gayophyti* Billings, in King Geol. Expl. 40th Par. **5**: 414. 1871.
*Aecidium pallidum* Schneid. Jahresb. Schles. Ges. 71. 1872.
*Puccinia Oenthoerae* Vize, Grev. **5**: 109. 1877.
*Aecidium Gayophyti* Vize, Grev. **7**: 12. 1878.
*Puccinia Boisduvaliae* Peck, Bot. Gaz. **7**: 45. 1882.
*Puccinia Gayophyti* Peck, Bot. Gaz. **7**: 56. 1882.
*Puccinia Clarkiae* Peck, Bull. Torrey Club **11**: 49. 1884.
*Puccinia Epilobii* Schroet. Pilz. Schles. **1**: 319. 1889.
*Puccinia intermedia* Diet. & Holw. Bot. Gaz. **18**: 254. 1893.
*Puccinia heterantha* Ell. & Ev. Erythea **1**: 204. 1893.
*Puccinia Eulobi* Diet. & Holw. Erythea **1**: 249. 1893.
*Aecidium Clarkiae* Diet. & Holw. Erythea **2**: 129. 1894.
*Puccinia Sphaerostigmatis* Diet. & Neg. Bot. Jahrb. Engler **22**: 353. 1896.
*Dicaeoma Boisduvaliae* Kuntze, Rev. Gen. Pl. $3^3$: 468. 1898.
*Dicaeoma Clarkiae* Kuntze, Rev. Gen. Pl. $3^3$: 468. 1898.

*Dicaeoma Gayophyti* Kuntze, Rev. Gen. Pl. $3^3$: 468. 1898.
*Dicaeoma heteranthum* Kuntze, Rev. Gen. Pl. $3^3$: 469. 1898.
*Dicaeoma intermedium* Kuntze, Rev. Gen. Pl. $3^3$: 469. 1898.
*Dicaeoma Oenotherae* Kuntze, Rev. Gen. Pl. $3^3$: 469. 1898.
*Puccinia Gayophyti* Speg. Anal. Mus. Nac. B. Ayres III. 1: 63. 1902.
*Puccinia Zauchneriae* Sydow, Monogr. Ured. 1: 435. 1903.
*Puccinia glabella* Holway, N. Amer. Ured. 1: 76. 1907.

O. Pycnia amphigenous, among or opposite the aecia, scattered, inconspicuous, subepidermal, honey-yellow becoming brown, globose, 85–150 $\mu$ in diameter by 110–170 $\mu$ in height; ostiolar filaments 30–65 $\mu$ long.

I. Aecia amphigenous, chiefly hypophyllous, scattered, from a diffused mycelium, numerous, often covering the entire leaf surface, cupulate or sometimes short-cylindrical, 0.2–0.5 mm. across; peridium white, margin recurved, lacerate; peridial cells rhomboidal, 13–22 by 22–36 $\mu$, overlapping, the outer wall 5–10 $\mu$ thick, striate, the inner wall thinner, 3–6 $\mu$, moderately verrucose; aeciospores irregularly globoid, angular, or ellipsoid, 13–20 by 13–23 $\mu$ (usually only to 20 $\mu$ in length); wall colorless, thin, 1 $\mu$, minutely verrucose.

II. Uredinia amphigenous, often only hypophyllous, numerous, scattered, occasionally confluent, roundish, small, 0.1–0.8 mm. across, rather early naked, pulverulent, cinnamon-brown, ruptured epidermis noticeable; urediniospores ellipsoid. obovoid, or globoid, flattened slightly on two opposite sides, 15–26 by 19–31 $\mu$; wall cinnamon-brown, thickness somewhat variable, 1.5–3 $\mu$, moderately or sometimes closely echinulate, the pores 2, equatorial, rarely slightly superequatorial, in lighter colored areas in the flattened sides.

III. Telia amphigenous, sometimes caulicolous, numerous, scattered or sometimes confluent, roundish, rather small, 0.2–1 mm. across, early naked, pulverulent or sometimes compact, dark chestnut-brown, ruptured epidermis inconspicuous; teliospores ellipsoid or obovoid, rounded or somewhat narrowed at one or both ends, somewhat variable upon different hosts, 14–27 by 23–50 $\mu$, usually somewhat constricted at the septum; wall cinnamon- or chestnut-brown, 1.5–3 $\mu$ thick, occasionally up to 4 $\mu$ thick, apex thicker, 4–12 $\mu$, sometimes finely and inconspicuously verrucose; pedicel pale, rather fragile, usually broken away, but sometimes twice the length of the spore.

On Onagraceae:

*Boisduvalia densiflora* (Lindl.) Wats., California, Idaho, Oregon, Washington.
*Boisduvalia densiflora imbricata* Greene, California.
*Boisduvalia glabella* (Nutt.) Walp., Idaho, Nevada, Oregon.
*Boisduvalia sparsiflora* Heller, California.
*Boisduvalia stricta* (A. Gray) Greene (*B. Torreyi* Wats.), Oregon.
*Chamaenerion latifolium* (L.) Sweet (*Epilobium latifolium* L.), Alaska.
*Chylisma cardiophylla* (Torr.) Small (*Oenothera cardiophylla* Torr.), California.
*Chylisma hirta* A. Nels., Nevada.
*Chylisma scapoidea scorsa* A. Nels., Idaho.
*Clarkia pulchella* Pursh, Idaho, Oregon, Washington.
*Epilobium adenocaulon* Hausskn., Montana, New Mexico, Washington; Alaskal
*Epilobium affine* Bong., Alaska.

*Epilobium clavatum* Trel. Montana.
*Epilobium minutum* Lindl., Oregon.
*Epilobium paniculatum* Nutt., California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, Wyoming.
*Epilobium perplexans* Trel., Idaho.
*Eulobus californicus* Nutt., California.
*Gayophytum caesium* Torr. & Gray, Idaho, Nevada, Utah, Wyoming.
*Gayophytum diffusum* Torr. & Gray, California, Idaho, Utah.
*Gayophytum lasiospermum* Greene, Utah.
*Gayophytum Nuttallii* Torr. & Gray, Idaho.
*Gayophytum racemosum* Torr. & Gray, Colorado, Idaho.
*Gayophytum ramosissimum* Torr. & Gray (*G. intermedium* Rydb.), Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Wyoming.
*Gayophytum* sp., Arizona, Washington.
*Godetia amoena* (Lehm.) Lilja, California.
*Godetia epilobioides* (Nutt.) Wats., Nevada, Washington.
*Godetia grandiflora* Lindl., California.
*Phaeostoma elegans* (Dougl.) A. Nels. (*Clarkia elegans* Dougl.), California.
*Phaeostoma rhomboidea* (Dougl.) A. Nels. (*Clarkia rhomboidea* Dougl.), California, Washington.
*Sphaerostigma andinum* (Nutt.) Walp. (*Oenothera andina* Nutt.), Idaho, Washington.
*Sphaerostigma bistorta* (Nutt.) Walp. (*Oenothera bistorta* Nutt.), California.
*Sphaerostigma Boothii* (Dougl.) Walp. (*Oenothera Boothii* Dougl.), Oregon, Washington.
*Sphaerostigma contortum* (Dougl.) Walp. (*Oenothera contorta* Dougl.), California, Washington.
*Sphaerostigma decorticans* (H. & A.) Small (*Oenothera gauraefolia* Torr. & Gray), California.
*Sphaerostigma dentatum* (Cav.) Walp. (*Oenothera dentata* Cav.), Oregon.
*Sphaerostigma hirtellum* (Greene) Small (*Oenothera hirtella* Greene), California.
*Sphaerostigma implexa* A. Nels., Idaho.
*Sphaerostigma micranthum* (Hornem.) Walp. (*Oenothera micrantha* Hornem.), California.
*Sphaerostigma pubens* (S. Wats.) Rydb. (*Oenothera strigulosa pubens* S. Wats.), California.
*Sphaerostigma spirale* (Lehm.) Walp. (*Oenothera spiralis* Hook.). California.
*Sphaerostigma utahense* Small, Utah.
*Sphaerostigma Veitchianum* (Hook.) Small (*Oenothera bistorta Veitchiana* Hook.), California.
*Sphaerostigma viridescens* (Lehm.) Walp. (*Oenothera viridescens* Lehm.), California.
*Taraxia brevifolia* Nutt., Montana.
*Taraxia graciliflora* (H. & A.) Raim. (*Oenothera graciliflora* H. &. A.), California.
*Taraxia heterantha* (Nutt.) Small, Wyoming.
*Taraxia longiflora* Nutt. (*Oenothera Nuttallii* Torr. & Gray), Nevada.

*Taraxia ovata* (Nutt.) Small (*Oenothera ovata* Nutt.), California.

*Taraxia subacaulis* (Pursh) Rydb. (*Oenothera heterantha* Nutt.), Colorado, Idaho, Montana, Nevada, Utah, Wyoming.

*Zauchneria californica* Presl., California.

*Zauchneria Garrettii* A. Nels., Utah.

TYPE LOCALITY: France, on *Epilobium tetragonum.*

DISTRIBUTION: From the western part of the Dakotas westward to the coast, and from Alaska to New Mexico and California; also (in part) in Europe, Asia, Australia, and South America.

ILLUSTRATIONS: Holway, N. Amer. Ured. 1: *pl. 33, f. 113a & b; pl. 34, f. 113c to e, 114, 115a & b; pl. 35, f. 115 c to h; pl. 36, f. 116 and 117.* Beitr. Krypt. Schweiz $2^2$: *f. 118.*

EXSICCATI: Barth. Fungi Columb. *2469, 2558, 2771, 3750, 3752, 4767*; Barth. N. Amer. Ured. *159, 295, 341, 356, 438, 439, 856, 953, 1148, 1252, 1262, 1350, 1359, 1440, 1579*; Clements, Crypt. Form. Colo. *561*; Ell. & Ev. Fungi Columb. *1851*; Ell. & Ev. N. Amer. Fungi *1846, 2986, 2995, 3139, 3140, 3477*, Garrett, Fungi Utah. *49, 50, 86, 92, 110, 145, 162, 173*; Sydow, Ured. *864, 865, 866, 874, 875, 881, 1063, 1064, 1768, 1918, 1919.*

As the synonymy indicates, some fifteen separately described and named long-cycled autoecious species of *Puccinia* upon the Onagraceae have been here combined as one species. Several of these names have been considered to be synonyms by different authors. For example, Holway considers *Puccinia pulverulenta* and *Puccinia intermedia* to be synonymous with *Puccinia Epilobii-tetragoni*, and *Puccinia Boisduvaliae*, *Puccinia Clarkiae*, *Puccinia Eulobi* and *Puccinia Sphaerostigmatis* to be hardly distinguishable from *Puccinia Oenotherae. Puccinia Gayophyti* has been described three separate times by independent authors. Other earlier repetitions in description, under the same names, are not included.

It was not without some hesitation that it was decided thus to combine all these forms. In first going over a few specimens of each species, for the sake of comparison, it was obvious that considerable differences existed. Some of the specimens showed dark, chestnut-brown teliospores, others lighter, cinnamon-brown; some specimens showed teliospores with scarcely thickened apices, others, thickened to 12 or 13 $\mu$; some were verrucose, others smooth; the size of these spores varied considerably. It seemed that surely several species of rust existed upon these hosts, as other workers had concluded; to consider combining them appealed to the writer as an easy and therefore inexcusable dodging of the issue. It was remembered, further, that this rust upon Epilobium occurs over most of the world; upon most of the other hosts, only in America. However, as the study

progressed, other considerations were forced upon the attention of the writer: as already noted, one has here to deal with closely related, variable hosts, and it is perhaps not strange that one should find the rusts also to be variable, and that the related American hosts should bear related rusts. In the course of the study here, between two and three hundred specimens of these autoecious rusts in the Arthur herbarium, assigned tentatively to different specific names, were examined. With the continuation of the work, it became more and more evident that the differences separating a few collections were neither of sufficient value nor constancy, as evidenced by an examination of a large number of collections, to render possible a division of species upon a morphological basis. A few examples may aid in corroborating this view.

The host Boisduvalia affords the most striking evidence of the variability of the rusts upon the Onagraceae. Holway, in his work upon the North American Uredineae, very logically described as a new species, *Puccinia glabella*, the rust occurring upon *Boisduvalia glabella* (Nutt.) Walp. This description was from a specimen distributed by Griffiths, West American Fungi 385, as *Puccinia Boisduvaliae* Peck. Holway points out that this rust upon *Boisduvalia glabella* is a very different thing from the rust occurring upon other species of *Boisduvalia: Puccinia glabella* has small teliospores (Holway gives 15–18 by 25–32 $\mu$), with the apex not at all or only slightly thickened; *Puccinia Boisduvaliae* possesses larger teliospores, usually much thickened at the apex. In a recent visit to the University of Wyoming, however. Dr. Arthur obtained further specimens of rusts upon Onagraceous hosts. Among these was a collection upon *Boisduvalia glabella* showing somewhat larger teliospores, with thicker apices, than was shown by other specimens in the herbarium upon this host. The measurements of the teliospores of this specimen of *Puccinia glabella* were 15–19 by 26–35 $\mu$, the apex 4–7 $\mu$. From the same herbarium a specimen was secured upon *Boisduvalia densiflora* (Lindl.) Wats., with spores but little larger, 16–23 by 32–39 $\mu$, and the apex the same thickness, 4–7 $\mu$. Another collection in the herbarium upon *Boisduvalia densiflora* shows teliospores 18–26 by 32–53 $\mu$, with the apex 7–12 $\mu$. That an error in identification of the host is not the explanation here, is indicated, not only by an examination of the material, and a consideration of the carefulness of the collectors, but by the fact that other specimens of Boisduvalia rusts

show similar variability; in fact, a gradual gradation is to be noted. Here then, the two extremes in these forms of Onagraceous rusts occur upon the same genus of host, to a great extent upon the same species, and shade by degrees the one into the other.

The genus Chylisma shows much variation in the rust upon different species; for example, a collection upon *Chylisma hirta* A. Nels. possesses teliospores 21–24 by 37–50 $\mu$, the wall chestnut-brown, smooth, the apex 7–11 $\mu$, the pedicel once or twice the length of the spore; another collection upon *Chylisma scapoidea scorsa* A. Nels. shows teliospores but 16–20 by 26–34 $\mu$, the wall from cinnamon- to chestnut-brown, appearing almost as if verrucose, the apex but 4–7 $\mu$ thick, the pedicel short.

The evidence obtained from the large number of collections points unquestionably toward great variability in morphological characters within the forms upon these Onagraceous hosts. In a general way differences are found between the rusts upon these different hosts which ordinarily may be utilized to indicate the placing of the rust within morphological races, as is indicated later in this article; yet specific distinctions, it seems to the writer, can not be drawn. It is significant that, in the work upon the correlated long-cycled autoecious Uromyces forms upon the Onagraceae, of which four species had been described, it was considered desirable also to combine them, as already published in the North American Flora.

The long synonymy involves some names about which confusion exists in the literature. The name *Aecidium pulchellum* Schrad. is omitted from the synonymy, being listed by DeCandolle as a synonym of his *Aecidium Epilobii* in Fl. Fr. **2**: 238. 1805. As no reference to any publication is given, it may be assumed that *Aecidium pulchellum* was a manuscript or herbarium name, never established. *Puccinia tenuistipes* Opiz is included on the authority of Sydow, who states that it occurs on *Epilobium hirtum* and is fully identical with *Puccinia Epilobii-tetragoni*. As listed by Opiz, Seznam Rost. Kvet. Ceske 139. 1852, one can hardly determine what is referred to. *Aecidium pallidum* Schneid. is also included on authority of Sydow (*l. c.*) also Schroeter (*l. c.*, p. 319), it having been found that Schneider erroneously determined his host plant, considering it to be *Lythrum Salicaria*, whereas Schroeter finds the host in reality to be *Epilobium hirsutum*.

*Puccinia Epilobii* DC. Fl. Fr. **6**: 61. 1815, is used by Saccardo,

Syll. Fung. **7**: 608. 1888, and by others, as the name for this species here considered as *Puccinia Epilobii-tetragoni*. The original *Puccinia Epilobii* of DeCandolle refers, however, to the short-cycled species still known under that name. Saccardo in Syll. Fung. **17**: 245. 1905, corrects the earlier mistake. Kuntze has made the combination *Dicaeoma Epilobii* Rev. Gen. **3**$^{3}$: 469. 1898, which name may be considered to be a synonym of the short-cycled *Puccinia Epilobii* DC.

The names *Uredo Epilobii* DC. and *Caeoma Epilobii* Link, included in the synonymy, have been particularly confused in the literature. Both these names have been used in the North American Flora as synonyms of *Pucciniastrum pustulatum* (Pers.) Dietel, and both have been used by the Sydows (Monog. Ured.) as synonyms both of *Pucciniastrum pustulatum* and *Puccinia Epilobii-tetragoni*. *Uredo Epilobii* is described by DeCandolle to take the place of his *Uredo vagans* var. *Epilobii-tetragoni*, which latter name he includes as a synonym. DeCandolle further says in his description that this Uredo is often found associated with *Aecidium Epilobii*, and he contrasts *Uredo Epilobii* with *Uredo pustulata* and *Puccinia Epilobii*. It is evident that this name in question refers to *Puccinia Epilobii-tetragoni* and not to a Pucciniastrum. *Caeoma Epilobii* is given by Link as having for synonyms *Uredo Epilobii* DC. and *Uredo vagans Epilobii* DC. (meaning *Uredo vagans Epilobii-tetragoni*, since he gives as reference Fl. Fr. **2**: 228). Link briefly describes *Caeoma Epilobii* as possessing ruptured epidermis surrounding, and as occurring upon *Epilobium tetragonum*. This name very evidently must be considered to be a synonym of *Puccinia Epilobii-tetragoni*.

*Caeoma Epilobiatum* is given by Link with *Aecidium Epilobii* DC. as a synonym. This Caeoma name has been used by the Sydows and others as a synonym of *Puccinia Epilobii-tetragoni*. It has also been used as a synonym of *Aecidium Circaeae* Cesati and Mont., as indicated previously in this paper. Link describes his species as "maculis oblitteratis," with a pseudoperidium, and orange or yellow spores, and as inhabiting leaves of Epilobium and Circaea in Europe. It would seem that, as Klebahn and others indicate, this name of Link may be used as a synonym of *Aecidium Circaeae* in part, and that it might refer also in part to *Puccinia Epilobii-tetragoni*.

The majority of the synonyms refer to descriptions made when this rust, with apparent differences, was found upon a new host, and to combinations made from these names. It is only when a large

number of collections are at hand that the value of the differences, indicated by the various descriptions, can be determined.

Some reasons for the continuation of the specific name *Epilobii-tetragoni* may not be out of place here. While used first as a varietal name, and resulting now in a long trinomial, its retention seems advisable in view of common usage and establishment by leading authorities. Furthermore, the two names following this in priority can scarcely be used, the Puccinia combination referring to a short-cycled form. Plowright and Grove have used the name *Puccinia pulverulenta* Grev., but this latter name is hardly in use outside of Great Britain.

Pycnia are not frequent in this species, since, as has been often pointed out, the aecial mycelium is perennial. Pycnia are found, it may be supposed, when infection with basidiospores occurs. Plowright (Monog. Ured. 152. 1889) states that in 1882 he obtained aecia from the sowing of aeciospores upon *Epilobium hirsutum*. Grove, however, doubts the validity of the result. Indeed, it is hardly to be expected that a rust should have two repeating spore stages; yet probably not beyond the bounds of possibility. Dietel (Flora **81**: 401. 1895) discusses this production of secondary aecia, and states that he obtained uredinia from sowing aeciospores. The aecia vary somewhat in shape, depending upon conditions, being sometimes short cylindric, usually cupulate, sometimes oval. The aeciospores vary slightly in size. It has been found rather infrequently that the aeciospores attain a length of 23 $\mu$, ordinarily being only up to 20 $\mu$ in length. This is especially true in cases in which uredinia or telia are present with the aecia. As far as can be determined from collections and studies thus far made, no definite distinction can be found between the aecia of *Puccinia Epilobii-tetragoni* and the aecia of *Puccinia Veratri*, save that the aeciospores of collections placed with the latter are ordinarily slightly larger, being more frequently up to 23 $\mu$ in length. These points are touched upon under *Puccinia Veratri* in this article.

It is, of course, possible that mixed infections may occur upon species of Epilobium. The aecia of *Puccinia Veratri* and the uredinia and telia of *Puccinia Epilobii-tetragoni* might easily be found occurring upon the same plant. Field collections of such infections would ordinarily be considered as only *Puccinia Epilobii-tetragoni*.

The uredinia and urediniospores are rather constant for this

species. Such variations as occur are considered in the discussion of the races.

The telia and teliospores show the greatest variation. It has been chiefly upon teliospore characters that specific differences have been previously indicated. Some telia are pulverulent, some more compact. There is considerable variation as to size of telia. The teliospores, in some collections and upon some species of host, are somewhat verrucose; the apical thickening, the size, the pedicel length, and in a measure, the color, likewise vary. While these variations are not altogether constant, some of them can be made use of in separating races, as is indicated later.

Holway (N. Amer. Ured. 1: 76) points out that *Puccinia Epilobii-tetragoni* shows a tendency to produce only aecia and telia at higher altitudes. This is a condition that has been previously observed with rusts. (See Magnus[8] and Fischer,[9] and further data under *Puccinia Epilobii-Fleischeri*.)

Intermingling of the perennial mycelium producing aecia and the local mycelium producing uredinia and telia, is frequently evidenced. So too, cases are found in which local gametophytic and sporophytic mycelia are intermingled, pycnia, aecia, and uredinia or telia or both, being sometimes found close together upon the same leaf. This point affords an opportunity for further study.

South American, European, and other foreign collections of this rust, upon Epilobium, as represented in the Arthur herbarium, show no morphological characters different from those of North American collections.

From the data at hand, as previously indicated, it appears that *Puccinia Epilobii-tetragoni* is a very variable species; these variations can be made use of in assigning morphological races to this species. To Mr. C. A. Ludwig thanks are due for a certain amount of the preliminary work pertaining to the separation of these races. The races are, in general, as follows:

1. *Puccinia Gayophyti* race. This race occurs upon Gayophytum (*Puccinia Gayophyti*) and Chamaenerion and Epilobium (*P. Epilobii-tetragoni*, *P. pulverulenta*, *P. intermedia*). The hosts of this race are very similar as to vegetative characters; so too are the forms of this

[8] Magnus, P., Bericht. Deutsch. Bot. Ges. 11: 453–464. 1893, and Hedw. Beibl. 39: 147–150. 1900.

[9] Fischer, Ed., Verh. Schweiz Nat. Ges. Luzern 88: 47. 1906.

rust which they bear. This race is quite uniform and unvariable, and almost of world wide distribution. The apex of the teliospore is, in this race, but moderately thickened, 3–7 μ, the wall cinnamon-brown, often finely verucose. Holway separates *Puccinia Epilobii-tetragoni* upon Epilobium from *P. Gayophyti* chiefly by the position of the germ pores of the teliospores, which in *Puccinia Epilobii-tetragoni*, as he considered the species, he finds are one or two in the lower cell, midway between the septum and base of the spore. This distinction in general holds, but has not been found of absolute constancy. This race is rather well correlated with the *Uromyces Gaurinus* race of *Uromyces plumbarius*.

2. *Puccinia glabella* race, on *Boisduvalia glabella*. But few specimens have been collected from this host. This race possesses the the smallest teliospores, 22–39 μ in length, with the apex but slightly thickened, 2–7 μ, the wall cinnamon-brown, rather paler below. The urediniospore have rather thick walls, 1.5–3 μ. This seems on the whole to be a good race, although many collections of the *Puccinia Gayophyti* race show characters quite as in this race, and other Boisduvalia rusts sometimes approach this.

3. *Puccinia heterantha* race, on Taraxia. This race is distinguished by thick walled teliospores, 1.5–3 μ, rather dark in color, cinnamon- to chestnut-brown, with the apex but moderately thickened, 3–7 μ. Considerable evidence of correlation between the *Uromyces Fremontii* race of *Uromyces plumbarius* is shown.

4. *Puccinia Oenotherae* race. On Boisduvalia [excepting *Boisduvalia glabella*] (*Puccinia Boisduvaliae*), Clarkia, Phaestoma (*Puccinia Clarkiae*), Chylisma, Godetia, Oenothera (*Puccinia Oenotherae*), Eulobus (*Puccinia Eulobi*), Sphaerostigma (*Puccinia Sphaerostigmatis*) and Zauchneria (*Puccinia Zauchneriae*). This group of hosts possesses rusts with thicker walled and darker teliospores, as in the preceding race, but with the apical thickening often greater, 4–12 μ, the thickening dark colored. The pedicel is sometimes up to 100 μ in length, the urediniospore walls thick. This race is correlated in particular with the *Uromyces Oenotherae* race of *Uromyces plumbarius*, although the *Uromyces plumbarius* and the *Uromyces Fremontii* races are not greatly different.

The above races of the species *Puccinia Epilobii-tetragoni* are not in all cases exactly correlated with the separate *Uromyces plumbarius* races, since no corresponding parallel of hosts, distribution, etc., fully

exists. The *Puccinia Oenothera* race differs from the *Uromyces Oenotherae* race only in the possession of two-celled teliospores. *Puccinia Epilobii-tetragoni* as a whole may well be said to be correlated with *Uromyces plumbarius* as a whole, as well as with *Puccinia Epilobii-Fleischeri*. The aecia in all three species are very similar to those of *Puccinia Veratri*. Possible correlations with short-cycled species of Puccinia are noted further with the discussion of such forms.

These races are separated out on morphological grounds, chiefly. Klebahn states (*l. c.*) that the biological identity of the forms upon different species of Epilobium, awaits proof; certainly the biological status of the collective species as here described, awaits study. The ultimate biological or physiological races may or may not follow these indicated morphological races; but it seems convenient at this time tentatively to designate such races.

*Puccinia Krookii* P. Henn., Ann. Naturhist. Hofmus. Wien for 1900: 1, described as on Epilobium sp., Harrysmith, Natal, and *Puccinia luxurians* Dietel & Neger, Engler's Jahrb. 24: 158. 1900, on *Oenothera mutica*, Cordillera de Santiago, Chile, present, in the descriptions, no distinctions that can be made use of in separating them from *Puccinia Epilobii-tetragoni* as here described. Both are listed in Sydow, Monog. Ured. Since no specimens are at hand for comparisons, however, their status cannot definitely be decided.

### 7. Puccinia Veratri Duby Bot. Gall. 2: 890. 1830.

Literature: Holway, N. Amer. Ured. 1: 21. 1905. Sydow, Monogr. Ured. 1: 639. 1903. Winter, in Rabenh. Krypt. Fl. 1: 184. 1881. Saccardo, Syll. Fung. 7: 665. 1888. Fischer, Beitr. Krypt. Schweiz $2^2$: 81. 1904. Oudemanns, Ann. Mycol. 2: 358. 1904. Tranzschel, Ann. Mycol. 7: 182. 1909. Klebahn, Krypt. Mark Brand. $5^a$: 338. 1914.

O. Pycnia hypophyllous, scattered between the aecia, immersed, becoming brownish, globose or flask shaped, rather large, 112–144 $\mu$ in diameter by 128–175 $\mu$ in height; ostiolar filaments 55–65 $\mu$ long; pycniospores many, oval, 0.5–1 by 1–3 $\mu$.

I. Aecia hypophyllous, numerous, crowded often over the entire lower surface of the leaf, broad cupulate, 0.3–0.6 mm. in diameter; peridium white, much recurved, the margin lacerate; peridial cells rhomboidal or oblong, 16–21 by 21–30 $\mu$, somewhat overlapping, the outer wall 3–5 $\mu$ thick, striate, the inner wall 3–6 $\mu$ thick, verrucose; aeciospores roundish or oval, 14–18 by 16–24 $\mu$; wall light yellow, thin, 1 $\mu$, finely verrucose.

On Onagraceae:

*Chamaenerion latifolium* (L.) Sweet (*Epilobium latifolium* L.), British Columbia.

*Epilobium alpinum* L., New Hampshire, Utah.
*Epilobium Hornemanii* Reich., Utah; British Columbia.
*Epilobium paniculatum* Nutt., Idaho; Washington.
*Epilobium rubricaule* Rydb., Utah.
II and III. Described in literature indicated.

Oudemanns (*l. c.*) has clarified the situation in regard to the author of this name, Niessel being often given credit for the name. So, too, Sydow's use of the name *Puccinia Veratri* Duby as a synonym for *Uromyces Veratri* (DC.) Schroet., is in error.

Tranzschel (*l. c.*) established the connection of the form with uredinia and telia on Veratrum with these aecia on Epilobium, obtaining his clue from the similarity of teliospores of this species with those of *Puccinia Epilobii.* In America it had for some time been noted that aecia occurred upon Epilobium without being followed by telia. These aecia agreed in general with the aecia of *Puccinia Epilobii-tetragoni*, however; they were therefore usually referred to that species. Actual cultures have not been reported for America showing the connection with *Puccinia Veratri* in such cases, but it seems logical to assume that such aecia are the alternate phase of this *Puccinia Veratri.* As noted in the discussion of *Puccinia Epilobii-tetragoni*, differences in aecia referred to these two species are small indeed. The aecia can scarcely be considered to be local. In truth, it has been more upon the fact that telia did not follow aecia, telia upon Veratrum being at hand, or sometimes because of proximity of collections of the two forms, that led to the aecial specimens being considered to be *Puccinia Veratri.*

Descriptions of the aecia for this heteroecious species have not been found in the literature.

There is a foreign Uromyces on Veratrum, with smooth teliospores and thickened apex, evidently not correlated with *Puccinia Veratri.*

8. PUCCINIA PECKII (DeToni) Kellerman, Journ. Mycol. **8**: 20. 1902.

O & I. Described as *Aecidium Oenotherea* by Peck in Rep. N. Y. State Mus. **23**: 60. 1873. (See Sacc. Syll. Fung. **7**: 790. 1888.)
II and III. On several species of Carex.

The aecia of this species have been found upon Gaura, Onagra, Merolix and Pachylophus from many parts of North America, especially from the central plains area. The aecia are distinguishable, especially from those of *Uromyces plumbarius*, which occur upon some

of the same hosts, by their local character. The aecia are rather large, the aeciospores up to 21 $\mu$ in diameter, with thin walls.

This species is shortly to be discussed in some detail by Kern.

As is indicated later in this article, the teliospores of this species, upon Carices, resemble the teliospores of certain other rusts upon the Onagraceae.

9. PUCCINIA JUSSIAEAE Speg., Anal. Soc. Cienc. Argentina **12**: 68. 1881.

(*Puccinia Ludwigiae* (Ell. & Ev.) Holway, N. Amer. Ured. **1**: 72. 1907.)

LITERATURE: Ell. & Ev., Proc. Acad. Phila. 155. 1893. Ell. & Ev., Bull. Torrey Club **22**: 363. 1895. Saccardo, Syll. Fung. **14**: 298. 1899; **21**: 627. 1912. (See also below.) Sydow, Monogr. Ured. **1**: 438. 1903. Spegazzini, references below.

Ellis and Everhart in 1895 described this Puccinia as on *Nesaea verticillata*, which was an error for *Ludwigia polycarpa*. (See Holway, *l. c.*) The name *Puccinia Nesaeae* was used, and perpetuated by Saccardo and Sydow. Ellis and Everhart had previously (1893), however, described the aecial stage of this fungus as *Aecidium Ludwigiae*.

This rust occurs upon various species of Ludwigia (Isnardia) in the central and southeastern portions of the United States.

With this species, formerly known as *Puccinia Ludwigiae*, is placed *Aecidium Jussiaeae* Speg. and *Puccinia Jussiei* Speg., making the name for this species *Puccinia Jussiaeae*. C. R. Orton, in working upon *Puccinia Ludwigiae*, discovered that the above rusts upon Jussiaea agree exactly, so far as can at present be determined, with the Ludwigia rust. Furthermore, Spegazzini states that the Aecidium is found associated with the Puccinia stage upon Jussiaea, thus making the rust one with the same life cycle as *Puccinia Ludwigiae*. Also, according to Engler and Prantl, Jussiaea and Ludwigia are very closely related and similar plants. *Aecidium Jussiaeae* was described in Anal. Soc. Cienc. Argentina **9**: 174. 1880; also in Saccardo, Syll. Fung. **7**: 790. 1888, and distributed by Spegazzini as Dec. Myc. Argentinae *30*. This specimen is in the herbarium here. *Puccinia Jussiei* was described in Anal. Soc. Cienc. Argentina **12**: 68. 1881; then in Sacc. Syll. Fung. **7**: 700. 1888. The hosts given are *Jussiaea lanceolata* and *Jussiaea longifolia*. No specimens of this Puccinia are at hand, but the description agrees almost exactly with that of *Puccinia Ludwigiae*.

To Mr. Orton are also due thanks for finding that *Aecidium Isnardiae* Lagerh. Tromso Mus. Aarsh. **17**: 102. 1895, described as upon leaves of Isnardia from Ohio, collector uncertain, belongs here. Isnardia is a synonym of Ludwigia. Farlow, Bibl. Index $1^1$: 59. 1905, gives some further data regarding *Aecidium Isnardiae*.

*Puccinia Jussiaeae* Speg., being the oldest name for this species, is, therefore, to be used.

This species, with long, narrow teliospores, does not show a correlation with *Puccinia Epilobii-tetragoni*. It is more definitely correlated with *Puccinia Circaeae*, as is discussed under the short-cycled species, in this paper.

10. PUCCINIA EPILOBII-FLEISCHERI Ed. Fischer, Bull. Herb. Boiss. 1897: 394. 1897.

LITERATURE: Saccardo, Syll. Fung. **14**: 299. 1899. Sydow, Monogr. Ured. **1**: 426. 1903. Fischer, Beitr. Krypt. Schweiz $2^2$: 154–155. 1904.

This species, known only from Europe upon *Epilobium Fleischeri* Hochst. (*Chamaenerion Fleischeri* Fritsch.) is without a uredinial stage. As Fischer (*l. c.*) states, it is nearly related to *Puccinia Epilobii-tetragoni*, excepting in the lack of uredinia. Fischer notes some small differences in the telial stages of the two species; yet this is no doubt correlated with *Puccinia Epilobii-tetragoni*, as previously indicated.

It seems to be established that uredinia do not occur in *Puccinia Epilobii-Fleischeri;* Fischer lists several collections bearing aecia and telia together. It is worthy of note that this species occurs at high altitudes, *i. e.*, in Switzerland. As already noted, uredinia of *Puccinia Epilobii-tetragoni* often occur less abundantly at higher altitudes in western North America. While no host-species of *Epilobium* has been found there which conspicuously lacks in the development of the uredinial stage, and while the evidence of the fixity of such a character in America is lacking, it is to be expected that a form agreeing with *Puccinia Epilobii-Fleischeri* may be found in the higher western portions of our continent.

Cultures have, apparently, not yet been made to decide just what the life cycle is in *Puccinia Epilobii-Fleischeri* under various conditions.

The short-cycled species of Puccinia upon the members of the Onagraceae present some difficulties. This is more directly due to the

fact that, of these forms, only *Puccinia Circaeae* has been collected in America in sufficient numbers to render its status definite. There is a considerable variation, in the morphological characters, between these different short-cycled forms. These characters appear to indicate evident relationships or correlations with different long-cycled species of rust upon the same or similar hosts. As is indicated under each species, and discussed further on in this article, these short-cycled forms appear to fall into two, very doubtfully three, general groups: the first, represented by *Puccinia Circaeae*, *Puccinia gigantea*, and *Puccinia Fuchsiae*, shows resemblance to *Puccinia Jussiaeae*. The second group, represented by *Puccinia Epilobii* and *Puccinia scandica*, shows a relationship to *Puccinia Veratri* and to *Puccinia Epilobii-tetragoni*. The third, represented by *Puccinia sphaeroidea*, is distinctive, but evidently does not in reality belong among the rusts of the Onagraceae.

11. PUCCINIA CIRCAEAE Pers. Tent. Disp. Fung. 39. 1797.

LITERATURE: Saccardo, Syll. Fung. 7: 686. 1888. Schroeter, Pilz. Schl. 1: 348. 1889. Sydow, Monogr. Ured. 1: 422. 1903. Fischer, Beitr. Krypt. Schweiz $2^2$: 319. 1904. Holway, N. Amer. Ured. 1: 79. 1907. Klebahn, Krypt. Mark Brand. $5^a$: 552. 1914.

This cosmopolitan species occurs upon all the species of Circaea present in North America, the rust probably being coextensive with the host. It frequently has been noted that the teliospores germinate both as a micro- and a lepto-Puccinia, depending upon the season.

The teliospores in this species are shorter and narrower than those of *Puccinia Jussiaeae*, yet it would seem that these are correlated species. The micro-form bears a greater resemblance to *Puccinia Jussiaeae* than does the lepto-form.

Schweinitz, Schr. Nat. Ges. Leipzig 1: 70. 1822, listed *Uredo Circaeae* as occurring in Carolina, then in Trans. Amer. Phil. Soc. n. ser. 4: 291. 1832, gave the name as *Caeoma Uredo Onagrarum* Link, and Pennsylvania also as a locality. The names he gives are now considered to refer to *Pucciniastrum Circaeae*, a species which does not occur, so far as is known, in North America. In both the above mentioned publications Schweinitz also lists *Puccinia Circaeae*. Further information is being sought from the Schweinitz herbarium in Philadelphia; until an examination of the original material is made, if such a thing be possible, it may not be unreasonable to assume that

the somewhat different appearance of this rust in the micro- and lepto-form, may have led to the supposition that an Uredo occurred upon Circaea.

12. PUCCINIA GIGANTEA Karst., Mycol. Fenn. 4: 42. 1878.

LITERATURE: Saccardo, Syll. Fung. 7: 669. 1888. Ellis & Everhart, Bull. Torrey Club 27: 60. 1900. Sydow, Monogr. Ured. 1: 428. 1903. Fischer, Beitr. Krypt. Schweiz $2^2$: 320. 1904. Holway, N. Amer. Ured. 1: 74. 1907. Klebahn, Krypt. Mark Brand. $5^a$: 553 (note). 1914.

Holway places with this species *Puccinia annulata* Ell. & Ev., both of which occur upon *Chamaenerion angustifolium* (L.) Schur. (*Epilobium angustifolium* L.). *Puccinia annulata* was described as possessing smaller teliospores, yet the two species no doubt go together, *Puccinia annulata* being but an American variation of the European *Puccinia gigantea*.

This species is not greatly different from *Puccinia Circaeae*, and appears to be correlated with *Puccinia Jussiaeae*. Only a very few collections are at hand, however.

13. PUCCINIA FUCHSIAE Sydow & Holway; Sydow, Ann. Mycol. 4: 30. 1906.

LITERATURE: Holway, N. Amer. Ured. 1: 79. 1907. Saccardo, Syll. Fung. 21: 627. 1912.

This species, as far as is known, has only been collected once, at Amecameca, Mexico. Sydow, *l. c.*, suggests that this species is much like *Puccinia Jussiaeae* from South America. It may, however, quite probably be a correlated short-cycled form. An examination of the original material discloses no very obvious difference from *Puccinia gigantea*. The host listed is *Fuchsia thymifolia*.

14. PUCCINIA EPILOBII DC., Fl. Fr. 6: 61. 1815.

LITERATURE: Schroeter, Pilze Schles. 1: 319. 1889. Sydow, Monogr. Ured. 1: 427. 1903. Saccardo, Syll. Fung. 17: 348. 1905. Holway, N. Amer. Ured. 1: 73. 1907. Bubak, Archiv. Naturw. Land. Boehmen 13: 148. 1908. Lind, Danish Fungi 318. 1913. Klebahn, Krypt. Mark Brand. $5^a$: 337. 1914.

This species, upon several species of Epilobium, is rather common in Europe. In America only two specimens referred to this species are known to have been collected (Holway, *l. c.*). Lind points out that the mycelium is perennial in the subterranean portions of the

the hots; sori are therefore scattered. The teliospores are verrucose, the walls usually uniformly 2 $\mu$ thick. As previously indicated, Klebahn directed attention to the similarity of these teliospores to those of *Puccinia Veratri*. While this micro-form thus corresponds with the long-cycled *Puccinia Veratri*, the relation with *Puccinia Epilobii-tetragoni*, especially with some collections possessing less thickened apices, is evident. The correlations thus evidenced, belong, then, to both the second and third types as indicated early in this paper.

15. PUCCINIA SCANDICA Johans., Bot. Centralbl. **28**: 395. 1886.

LITERATURE: Saccardo, Syll. Fung. **7**: 680. 1888. Sydow, Monogr. Ured. **1**: 427. 1903. Holway, N. Amer. Ured. **1**: 73. 1907.

Specimens referred here have been collected a few times in North America. The chief difference from *Puccinia Epilobii* is in the smaller size of the teliospores, and the rather thicker apices, in collections considered to be *Puccinia scandica*. *Epilobium alpinum* and *Epilobium clavatum* are the hosts known in North America. *Epilobium alpinum* is also an American host for what is considered to be *Puccinia Epilobii*. While the differences between these two short-cycled rusts appear to hold for North America so far as the few collections are concerned, further collections may possibly indicate that these two species belong together. This species shows more definitely the correlation with *Puccinia Epilobii-tetragoni*, especially the race upon Epilobium, and may also be considered to be correlated with *Puccinia Veratri*.

16. UREDO OENOTHERICOLA Speg., Anal. Mus. Nac. B. Aires **19**: 318. 1909.

LITERATURE: Saccardo, Syll. Fung. **21**: 794. 1912. Spegazzini, Anal. Mus. Nac. B. Aires **23**: 32. 1912.

Spegazzini described this rust upon *Oenothera mollissima*, from South America. He refers again to it in his later publication cited. No specimens have been seen by the writer. No clues are evident from his description. What the significance is, of his statement "pedicello hyalino mox fatiscente (40–50 $\mu$ lng. 5 $\mu$ crss.) saepe suffultae," is a question. It is not impossible that this rust may be the uredinial stage of some previously noted rust upon Oenothera.

## Doubtful Species

17. Puccinia sphaeroidea P. Henn. Hedwigia 42: (107). 1903.

Literature: Sydow, Monogr. Ured. 1: 890. 1904. Saccardo, Syll. Fung. 17: 348. 1905. Holway, N. Amer. Ured. 1: 72. 1907.

This species, cited as upon Jussiaea sp., Lower California, differs markedly from any other rust upon the Onagraceae. The collection by Purpus, 1902, is the only one known. The specimen represented in the herbarium here is very fragmentary. The teliospores are ovoid, the wall uniformly thick, the pedicel persistent, often inserted laterally. These teliospores exactly resemble those of *Puccinia sphaerospora* Sydow and Henn., the hosts of which are Asclepiadaceous plants. Sections of the material indicate that the host is quite likely in reality some Asclepiad. The characteristic spores point strikingly toward such a conclusion. On the whole, this species seems most doubtfully to belong with the Onagraceous rusts.

## Excluded Species

Puccinia columbensis Ell. & Ev Proc Acad. Phila. 1893: 153. 1893.

Stated to be upon *Oenothera biennis*. Holway, Journ. Mycol. 8: 171. 1902, points out that the host of this Puccinia is Troximon, not Oenothera. An Aecidium labeled as upon the same host, proved to be upon *Solidago mollis* and the rust is described by Arthur, Bull. Torrey Club 31: 7–8. 1904, as *Aecidium recedens*. See also Sydow, Monogr. Ured. 1: 869. 1904.

Uromyces intricatus Cooke, Grev. 7: 3. 1878.

Stated to be upon *Gayophytum ramosissimum*. The host, however, proves to be Eriogonum. See N. Amer. Fl. 7: 244–245. 1912.

During the progress of this study, Professor Jackson obtained from the phanerogamic herbarium of the Field Museum, Chicago, a specimen (on Jussiaea sp., marsh land near Ferry River, vicinity of Kingston, Jamaica, Sept. 11–12, 1906, N. L. Britton, No. 397) which bears a very few small uredinial sori. The urediniospores are ellipsoid, 19–23 by 26–29 $\mu$, the walls golden-brown, 1–2 $\mu$ thick, moderately echinulate, with equatorial pores. The known Jussiaea rusts are not believed to have an uredinial stage, but some Onagraceous rust, as for instance *Uromyces plumbarius*, may possibly occur upon Jussiaea.

The material is so scanty and the uncertainty so great, however, that one can only direct attention to this point.

As is to be expected, several genera of the Onagraceae are not known to be attacked by rusts. No other species of rust, than those herein listed, appear at present to be known to occur upon the Onagraceae.

As is stated in the beginning of this paper, the Sydows list 27 species of rust upon the Onagraceae, and 4 additional species occur in North America. Furthermore, the Sydows have not yet published the species *Aecidium Jussiaeae*, *Aecidium Circaeae*, and *Uredo oenotherícola*. These 34 species are accounted for in this article under 17 titles. The arguments for this halving of the number of species are presented wherever a union is involved. Furthermore, a few other species are suggested as being of doubtful validity, notably numbers 16 and 17. It is suggested that the two races exist under the title *Pucciniastrum pustulatum* as herein treated.

Cultural data is necessarily of importance in limiting species and races; such data is at hand for but few of these rusts. The writer submits the foregoing arrangement of species, based upon a consideration of morphological characters and life histories, as well as hosts, distribution, and such limited cultural data as is at hand, in the hope that a workable arrangement may be presented. Finality of placement, is, of course, at the present time impossible.

The Onagraceae rusts, as far as the evidence in hand can be analyzed by the writer, appear, as partially indicated heretofore, to fall into three fairly definite groups, with an uncertain fourth group. (See the diagram.) The first is that of the Pucciniastrums, with the alternate stage, insofar as cultures have been successful, upon Abies. The morphological characters of the uredinial and telial stages upon Onagraceous hosts, are very similar within the different species of Pucciniastrum. They, however, can scarcely be construed to hint at any relation with the uredinial or telial stages of others of these rusts upon the same or similar hosts.

Following the suggestion of Dietel[10] that the Uredinales have developed during geologic times with their hosts, the Pucciniastrums would be the oldest of these rusts, since their aecial stage, so far as

[10] Dietel, P., Centr. Bakt., etc. $12^2$: 218–234. 1904, and Hedwigia 48: 118–125. 1908.

is known, occurs upon Gymnosperms. The telial stage further suggests a more primitive condition, resembling the fern rusts, which Dietel considers to be the oldest rusts. The genera Epilobium and Chamaenerion, the hosts of these species of Pucciniastrum, might therefore be considered to be older genera of the Onagraceae. Other facts, as indicated elsewhere in this article, point to the same conclusion. It is further to be noted that these two hosts harbor more species of rust than any other genera of the Onagraceae, including two heteroecious species, two autoecious long-cycled species, one with and one without uredinia, and three short-cycled species.

The second group is that including the long-cycled species *Uromyces plumbarius* and *Puccinia Epilobii-tetragoni*, and also the heteroecious species with its aecia upon the Onagraceae, *Puccinia Veratri*, the European species without uredinia, *Puccinia Epilobii-Fleischeri*, and the short-cycled species *Puccinia Epilobii* and *Puccinia scandica*. The morphological resemblances between the several species is so close that it seems quite logical to infer a relationship.

*Uromyces plumbarius* and *Puccinia Epilobii-tetragoni* differ but little in morphological characters in all the spore forms, save for the occurrence of one-celled and two-celled teliospores respectively. In other respects, however, the correlation does not hold as it does between certain other parallel species of Uromyces and Puccinia, for here a different set of hosts is attacked by the two species in question, and the geographical range of *Uromyces plumbarius*, while largely including that of *Puccinia Epilobii-tetragoni*, extends far beyond it, the Puccinia species being, in North America, wholly western, the Uromyces extending over the greater part of the United States. It is a curious fact that, so far as is known, the same species of host is not attacked by the two rusts. Indeed, unless they may meet upon the genera Oenothera, different host genera are attacked, that is, different genera as now subdivided. Twelve genera of the Onagraceae are given as hosts for *Puccinia Epilobii-tetragoni;* and seven genera as hosts for *Uromyces plumbarius;* while related genera obviously occur in the two sets, yet all are different. While deductions must be vague, this fact would seem at least to indicate that a rather definite and distinct specialization has arisen within these two species of rust. It might be inferred further that this specialization has occurred in a somewhat different way in each species; in the *Puccinia*, over a larger number of host genera, but limited geographically, in North America, to the

west; in the Uromyces, over a greater area of North America, but limited to fewer hosts. *Uromyces plumbarius* also shows less variation than does *Puccinia Epilobii-tetragoni;* this is rather to be expected. An apparently complicating factor is that of the occurrence of this Puccinia upon various species of the genus Epilobium in some part of every continent, doubtfully excepting Africa. This is, however, in line with other relations of these rusts to the genus Epilobium, as is noted elsewhere. The variable American hosts are followed by variable rusts; this variability is further indicated by the fact that species of Uromyces occur only in America. Indirectly, it seems to the writer, the sharp difference in host genera attacked by the two above rusts reflects a considerable accuracy of taxonomic arrangement of hosts.

*Puccinia luxurians* and *Puccinia Krookii*, as stated, may be included with *Puccinia Epilobii-tetragoni.*

The relations of *Puccinia Veratri*, with aecia upon Epilobium, and of the other species of this group, has been indicated, and scarcely needs further comment. *Puccinia Veratri* has a more extended distribution than has *Puccinia Epilobii-tetragoni.* What conclusions are to be drawn from the comparatively greater frequency, but more limited distribution, of *Puccinia Epilobii-tetragoni*, as compared with the evident rarity, yet, in America, broader distribution of the short-cycled *Puccinia Epilobii* and *Puccinia scandica*, the writer is not prepared to say.

Into the third group may be placed *Puccinia Jussiaeae, Puccinia Circaeae, Puccinia gigantea, Puccinia Fuchsiae*, and *Puccinia Peckii.* The teliospores in this group are easily distinguishable from those of the group mentioned in the preceding paragraphs, being longer and narrower, often paler. Here, too, this similarity exhibited is close enough through all the species of this group to suggest a relation. *Puccinia Peckii* bears the same relation to this group that *Puccinia Veratri* does to the preceding group. As *Puccinia Veratri* is more extensive in range, in North America, than is *Puccinia Epilobii-tetragoni*, so *Puccinia Peckii* has also a more extended range than has *Puccinia Jussiaeae.* The hosts of the two latter species are in no cases identical, in spite of an evident relationship. This third group lacks, as far as known, a representative with uredinia upon the Onagraceae. While, of the short-cycled species in this group, *Puccinia gigantea* and *Puccinia Fuchsiae* appear to be more rare, *Puccinia Circaeae* is common.

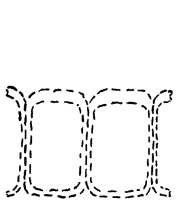
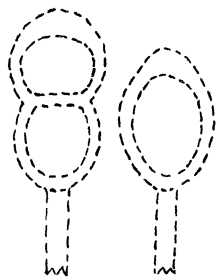
Into the fourth group must be placed the unknowns, *Aecidium Anograe*, *Aecidium Circaeae*, and *Uredo oenothericola*. (*Puccinia sphaeroidea*, as discussed previously, may be here omitted.) *Uredo oenothericola* may eventually land in the second group here given. Applying certain principles of correlation that have sometimes proven serviceable heretofore, one might vaguely prophesy regarding the alternate stages of *Aecidium Anograe* and *Aecidium Circaeae*. These two forms stand rather at extremes of the heteroecious aecial stages upon the Onagraceae. *Aecidium Anograe* has the largest aeciospores, and is the only one known possessing thick walls. *Aecidium Circaeae* has the smallest aeciospores, with thin walls. The former might be prophesied to go with an alternate form possessing rather large, thick-walled urediniospores; the latter, perhaps, with a form having small urediniospores.

Taking up the relation of these rusts to their hosts, a few points of interest are evident, in addition to those already presented in other connections. The related and cosmopolitan genera Chamaenerion and Epilobium harbor rusts that are placed in the first three groups just discussed. That there is some relation between the wide distribution, and, possibly, greater age of these genera, and the many, varied, and widely distributed rusts parasitic upon them, readily suggests itself. The most anomalous thing here appears to be the occurrence of the one representative of our third group, *i. e.*, *Puccinia gigantea*.

Another point with respect to hosts, rather out of harmony with expectations, is the conspicuous identity of the hosts of the different races of *Uromyces plumbarius* and those of the aecia of *Puccinia Peckii*. These two are not correlated species; and, indeed, as noted, neither of the two inhabits a host genus upon which an apparently correlated species does occur. The significance of this point seems perplexing to the writer.

Throughout these rusts upon the Onagraceae, wherever collections are in hand in sufficient numbers for a considerable comparison, variability is to be noted. Although short-cycled species are often found to be more constant, yet in the Onagraceae, the one American short-cycled species that is well represented in the Arthur herbarium has been found variable; it exists as a micro- or lepto-form in different seasons; the characters of the sori and teliospores vary. *Puccinia Jussiaeae* shows considerable variation. The marked variability of the autoecious species has been noted. One rather outstanding feature with

TABLE TO ILLUSTRATE THE GROUPS INTO WHICH THESE RUSTS FALL, WITH ALTERNATE HOSTS INDICATED WHERE KNOWN, AND DIAGRAMS OF THE GENERAL CHARACTER OF THE TELIOSPORES

| 1 | 2 | 3 | 4 |
|---|---|---|---|
| Teliospores Adherent in Layers | Teliospores Free, Short-ellipsoid | Teliospores Free, Long-ellipsoid | |
|  |  |  | (Probably Belong with Column 2 or 3, or Both) |
| II, III<br>*Pucciniastrum pustulatum*<br>(O and I unknown) | O, I, II, III<br>*Uromyces plumbarius*<br>*Puccinia Epilobii-tetragoni* | O, I, III<br>*Puccinia Jussiaeae* | O, I<br>*Aecidium Anograe*<br>*Aecidium Circaeae* |
| (*P. Abieti-chamaenerii*<br>O and I on Abies) | (O), I, III<br>*Puccinia Epilobii-Fleischeri* | (O), III<br>*Puccinia Circaeae*<br>*Puccinia gigantea*<br>*Puccinia Fuchsiae* | II<br>*Uredo oenothericola*<br>(Other stages of the above unknown) |
| *Pucciniastrum Circaeae*<br>(O and I unknown) | (O), III<br>*Puccinia Epilobii*<br>*Puccinia scandica* | | |
| | O, I<br>*Puccinia Veratri*<br>(II and III on Veratrum) | O, I<br>*Puccinia Peckii*<br>(II and III on Carex) | |

regard to the variability of these rusts is the comparative constancy, in spite of wide distribution, of the several rusts upon the related genera Epilobium and Chamaenerion. This fact, with others, it seems to the writer, indicates that the variability of the rusts upon the Onagraceae, as similarly noted by Dr. Arthur with the rusts upon the Rosaceae, reflects the variability of the hosts themselves. Indeed, the evolution of these hosts and their rusts would appear to present many parallelisms.

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## Index to Hosts and Rusts on Onagraceae